

Review of the World Species of *Sigalphus* (Hymenoptera: Braconidae: Sigalphinae) and Biology of *Sigalphus romeroi*, New Species

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Abstract.—Two new species, *Sigalphus romeroi* Sharkey from Costa Rica and *Sigalphus masoni* Sharkey from Nepal, are described. The world species are reviewed, a key to the world species is presented, and the life history of *Sigalphus romeroi* is described.

INTRODUCTION AND HISTORICAL REVIEW

Until recently, there has been little research done on the species of *Sigalphus*. The pre-1973 literature on *Sigalphus* is catalogued in Shenefelt (1973). The more recent literature is summarized here. Tobias (1974) described *Sigalphus mongolicus* from Mongolia. You, Zhou and Tong (1991) described two putative new species of *Sigalphus* from Hunan Province of China, viz. *S. hunanus* You and Tong and *S. anomis* You and Tong. Achterberg and Austin (1992) reviewed the world species of *Sigalphus* Latreille and revised the world genera of Sigalphinae. Five species of *Sigalphus* were recognized, viz., *S. bicolor* (Cresson), *S. fulvus* Brues, *S. irrorator* (Fabricius), *S. neavei* (Turner), *S. testaceus* Granger. *S. Hunanus* and *S. anomis* were synonymized with *S. irrorator*. Achterberg and Austin apparently overlooked *S. mongolicus* Tobias (1974). He and Chen (1993) described two new species from China, *Sigalphus flavistigmus* He and Chen and *Sigalphus nigripes* He and Chen. You and Zhou (1994) revised the Chinese species of *Sigalphus*. They disagreed with Achterberg and Austin's (1992) synonymies and elected to reestablish *S. hunanus* and *S. anomis*,

suggesting that these two may represent only one species. He, Chen, and Ma (1994) synonymized *S. anomis* and *S. nigripes* under *S. hunanus* and described two new species, i.e., *S. gyrodontus* He and Chen and *S. rufiabdominalis* He and Chen.

In the present paper the world species are reviewed; a key to the world species of *Sigalphus* is presented incorporating two new species, and the life history of *Sigalphus romeroi* n. sp. is described.

Sigalphus can be distinguished from all other genera of Braconidae by the presence of the following combination of characters: metasomal terga 1 to 3 forming a carapace, with a free articulation between metasomal segments 1 and 2 (Fig. 1); hind wing with vein 2CU present and very posterior in position such that the crossvein cu-a is less than $.2 \times$ the length of vein 1CU (Figs 3b).

Although this paper is co-authored, the senior author is the sole authority of the new species of *Sigalphus*, the junior author is responsible for the biological data of *S. romeroi*.

Although widespread, *Sigalphus* has few species; intensive collecting in the New World by members and associates of the Hymenoptera Section of the Canadian Na-

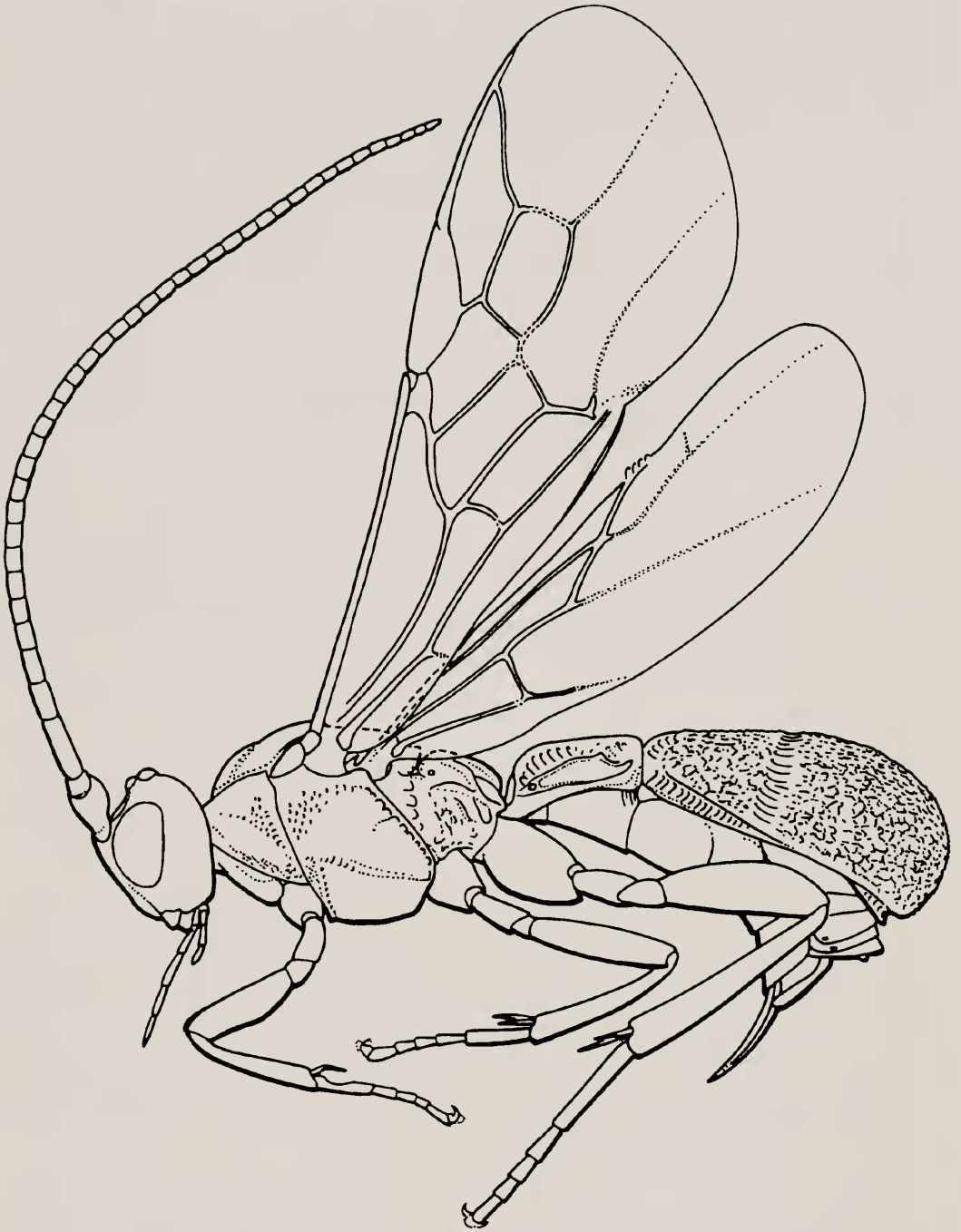


Fig. 1. Lateral aspect of *Sigalphus bicolor*.

tional Collection of Insects, has yielded no new species, and none have been found in the world's major collections. Generally specimens do not appear to be rare, for example *S. bicolor* and *S. irrorator* are well represented in the best North American and European collections. The discovery of a new species in Costa Rica (*S. romeroi*) may be the last such discovery in the New World.

SYNONYMIES

Having seen the type species of both *S. hunanus* You and Tong and *S. anomis* You and Zhou, the senior author agrees with Achterberg and Austin (1992) that they are both junior synonyms of *S. irrorator*. In a recent paper He and Chen (1993) proposed two new species both of which the senior author also considers to be junior synonyms of *S. irrorator*. Although the type specimens have not been made available to the senior author (several requests were made), it is clear from the description that *Sigalphus flavistigmus* He and Chen is a junior synonym of *S. mongolicus*. These two nominal species have similar color patterns except that *S. mongolicus* has the first and second metasomal terga reddish yellow whereas only the second metasomal tergum of *S. flavistigmus* is reddish yellow. Based on color variation in members of *S. bicolor*, of which the senior author has seen a large series of individuals, the color difference between *S. mongolicus* and *S. flavistigmus* is well within the probable range of intraspecific variation. Not only are there no structural characters that sufficiently separate the two species, but the unique specimens of each supposed species were found in close proximity to each other, i.e., north central China and Mongolia, further supporting their conspecific identity. In their recent revision of the Chinese species, He et al. did not consider *S. mongolicus*. It is the senior author's opinion that *S. mongolicus* itself is likely synonymous with *S. irrorator* because they apparently differ only in col-

or characters and trivial morphological characters. This decision will await an examination of the types and a more complete investigation of color variability in *S. irrorator*.

He and Chen (1993) also described *Sigalphus nigripes* which the senior author, in accord with He et al. (1994), considers to be a junior synonym of *S. irrorator*. He and Chen (1993) stated that it is very similar to *S. anomis*, and indeed, it is. The characters of relative lengths of various veins and body parts that were used to separate the two supposed species are insignificant when compared to the intraspecific variation found in both *S. irrorator* and *S. bicolor*. According to He and Chen (1993), one specimen of *S. nigripes* was reared from *Anomis flava* (Noctuidae), the same host species from which the unique specimen of *S. anomis* was reared. This shared host further supports the proposed synonymy of *S. nigripes*. In the most recent of the papers published in China, He et al. (1994) considered *S. nigripes* and *S. anomis* to be junior synonyms of *S. hunanus*.

The senior author is dubious about the specific status of the two new species described by He et al. (1994) as these may also be junior synonyms of *S. irrorator*. Both of these nominative species share with *S. irrorator* (including those entities synonymized with *S. irrorator*) a unique state of sculpture on the second metasomal tergum. This is a central longitudinal groove, which is bordered by two carinae. This groove is divided medially by a weak central keel and the entire depression is areolate-rugose. *S. gyrodontus* and *S. rufiabdominalis* differ from specimens of *S. irrorator* that the senior author has seen in that the two spines at the apex of metasomal tergum 3 are not as sharp as those of *S. irrorator*. The variation in this character in *S. irrorator* does not appear to be great, but series of specimens from the east Palearctic must be checked. These two species are therefore provisionally accepted.

PHYLOGENETIC CONSIDERATIONS

No hypothesis of the phylogenetic relationships of *Sigalphus* species has been published. Achterberg and Austin (1992) analyzed the genera of the Sigalphinae. Despite this valiant first attempt at approximating relationships among the genera, the monophyly of *Sigalphus* is questionable due to the inclusion of the Ethiopian species (*S. fulvus*, *S. testaceus*, and *S. neavei*). Achterberg and Austin (1992) in their cladogram of sigalphine genera cite 4 synapomorphies for the genus; they are all suspect. These will be treated here in the order they appear on the cladogram.

1. "Third tergite with lobes or teeth ventro-posteriorly." This character state is not possessed by any of the three Ethiopian species, conversely it is found in all members of *Aposigalphus* and *Notosigalphus* in a condition almost identical to that of *S. romeroi* (Fig. 2a). Although the character state appears on the cladogram of Achterberg and Austin it is not included in their data set. Species of *Minanga* also have teeth ventro-posteriorly on the third tergum but since these do not emanate from the margin of the tergum as they do in the aforementioned groups their homology is doubtful. The character state has three possible origins given the phylogeny of Achterberg and Austin, viz. a) a synapomorphy for *Sigalphus* + (*Aposigalphus* + *Notosigalphus*) with a loss in the Ethiopian species of *Sigalphus*, b) a synapomorphy for the non-Ethiopian species of *Sigalphus* and a synapomorphy (convergence) for *Aposigalphus* + *Notosigalphus*, or c) a synapomorphy for *Minanga* + (*Sigalphus* + (*Aposigalphus* + *Notosigalphus*)) with a loss in the Ethiopian species of *Sigalphus*. This last hypothesis assumes that the condition in *Minanga* and the other genera is homologous. None of these character state distributions provides support for the concept of *Sigalphus* including the Ethiopian species.

2. "Strongly costate metapleuron." This

is another character that was not included in the Achterberg and Austin data set but rather it was added to the cladogram a posteriori. An assessment of the distribution of this character state shows that the metapleura of the non-Ethiopian species of *Sigalphus* are relatively more costate than those of the Ethiopian species which are mostly rugose, as in species of *Minanga* and *Acampsis*. Again, this character state does not support the monophyly of *Sigalphus*.

3. "First tergite with complete and strong dorsal carina." Although this character state is included in the data matrix, the cladogram does not present the most parsimonious distribution. The data matrix lists the following taxa as possessing the derived character state: *Sigalphus*, *Minanga*, *Acampsis*, and *Afrocampsis*. This distribution is correct, but on the cladogram Achterberg and Austin indicated that the character state is an autapomorphy for *Sigalphus* and ignore the rest of the character state distribution. There are several parsimonious reconstructions of the character but all indicate that the presence of strong dorsal carina on the first tergite is plesiomorphic with reference to *Sigalphus*.

4. "Face with shallow semicircular depression." This depression apparently refers to the two longitudinal depressions that define the raised medial area of the face. Some specimens of *S. irrorator* appear to have these depressions somewhat expanded laterally but in other species of *Sigalphus* there is no discernable difference between these depressions and those of most other genera of Sigalphinae except *Afrocampsis* which does not have them.

In summary, there is no evidence for the monophyly of *Sigalphus* as presently defined. That all four of the putative synapomorphies proposed by Achterberg and Austin are incorrect suggests that their entire analysis is suspect. We do not wish to address generic concepts in this paper, only to draw attention to the fact that care must be taken in interpreting their re-

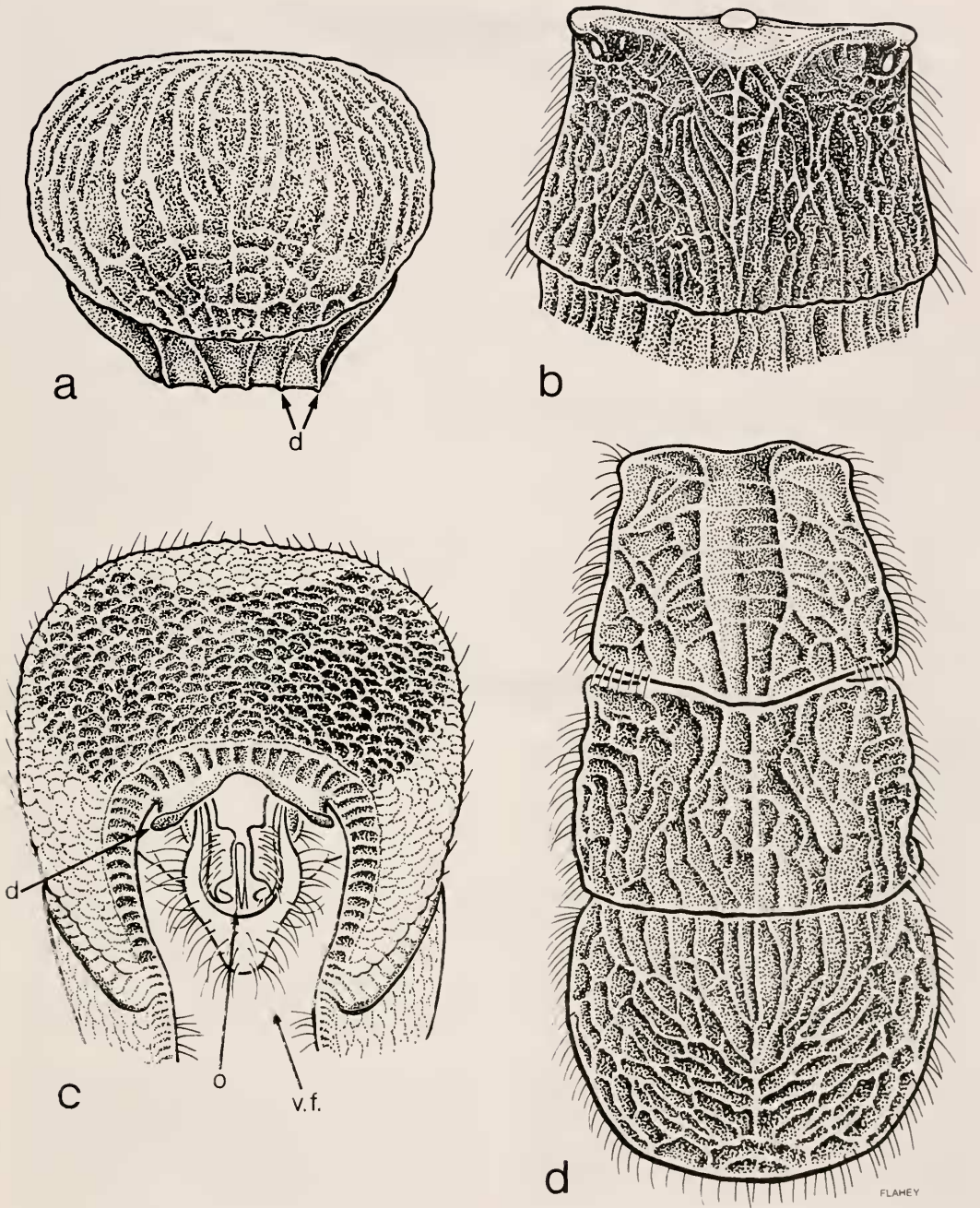


Fig. 2. a, posterior aspect of metasoma of *Sigalphus romeroi* showing ridges on ventral apex (d = denticles); b, dorsal aspect of metasomal tergum 2 of *Sigalphus masoni*; c, posteroventral aspect of metasoma of *Sigalphus masoni* showing denticles at ventral apex (d = denticles, o = ovipositor, v.f. = ventral foramen); d, dorsal aspect of metasoma of *Sigalphus romeroi*.

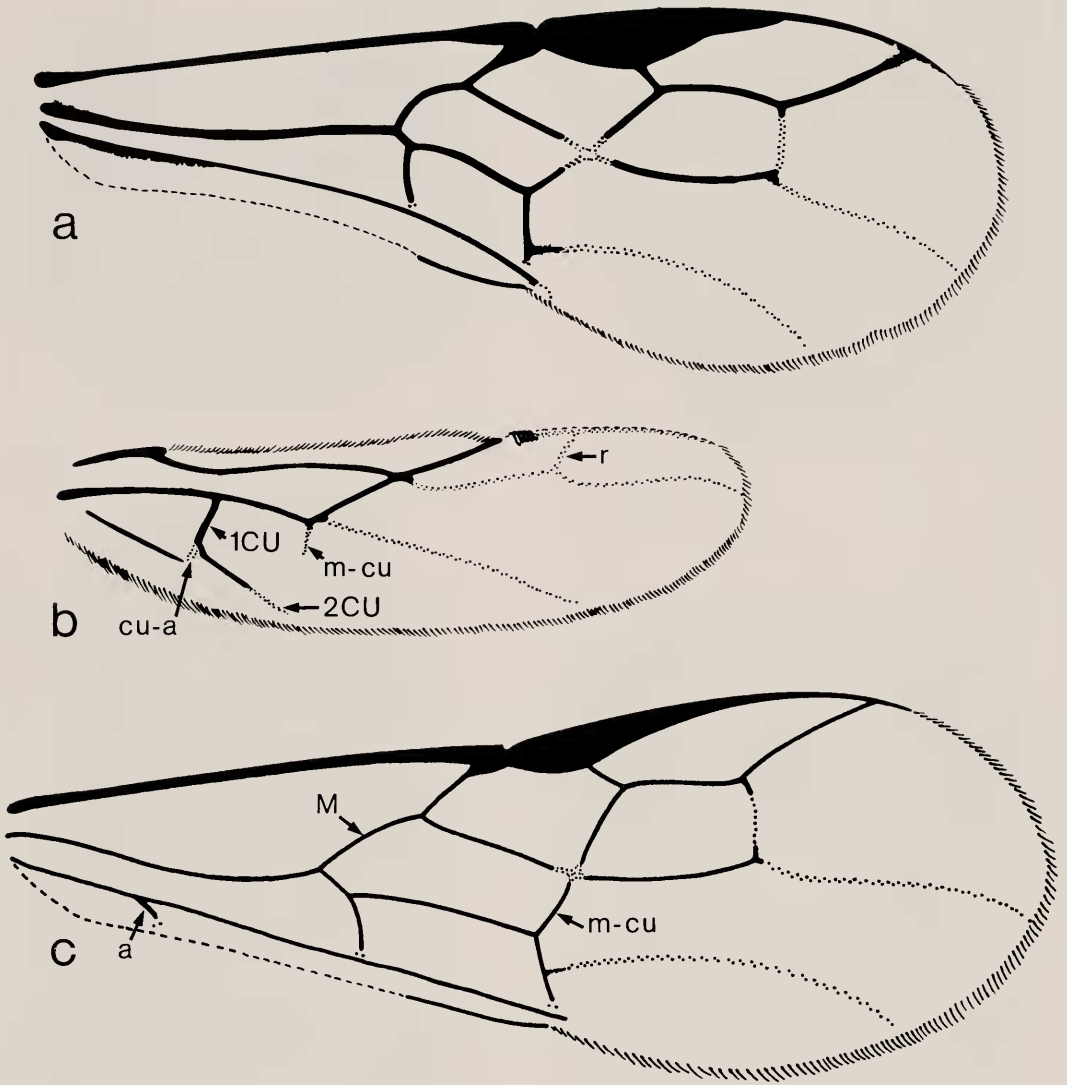


Fig. 3. a, fore wing of *Sigalplus romeroi*; b, hind wing of *Sigalplus romeroi*; c, fore wing of *Sigalplus masoni*.

sults. A phylogenetic analysis of the species of *Sigalplus* must be preceded by a reexamination of the relationships of the genera and this is beyond the scope of this

paper. The non-Ethiopian members of *Sigalplus* may be monophyletic, based on the presence of denticles at the ventroposterior margin of tergum 3.

KEY TO WORLD SPECIES OF *SIGALPHUS*

- 1. New World species. 2
- 1' Old World species. 3
- 2. Metasoma orange; posterior flange of ventral foramen of metasoma smooth apically, ridges reduced to small crenulae not reaching apex of flange (south eastern Canada and eastern U. S. A. south to Florida). *S. bicolor* (Cresson)

- 2'. Metasoma black; posterior flange of ventral foramen of metasoma with ridges extending to apex (Fig. 2a) (known only from the type locality in northwestern Costa Rica, but the two species of noctuid hosts occur throughout the Mesoamerican Pacific dry deciduous forest and this parasitoid may be found there as well) *S. romeroi* n. sp.
- 3. Head and mesosoma entirely black 4
- 3'. Head and mesosoma not entirely black, rather with pale coloration 9
- 4. Apex of ventral foramen of metasoma lacking denticles and two rounded lobes (southern Africa) *S. neavei* (Turner)
- 4'. Apex of ventral foramen of metasoma with two denticles or two rounded lobes (Fig. 2c) (Oriental, Palearctic) 5
- 5. Apex of ventral foramen of metasoma with two sharp denticles 6
- 5'. Apex of ventral foramen of metasoma with two rounded lobes 7
- 6. Metasoma entirely black; stigma black (Palearctic) *S. irrorator* (Fabricius)
- 6'. Metasoma orange and black; stigma yellow (Mongolia and northern China) *S. mongolicus* Tobias
- 7. Tergum 2 with two parallel median longitudinal carinae with a median longitudinal groove between them 8
- 7'. Tergum 2 without two parallel median longitudinal carinae and without a median longitudinal groove *S. masoni* n. sp.
- 8. Fore wing entirely melanic-infusate; tergum 3 as wide as tergum 2 *S. gyrodontus* He and Chen
- 8'. Fore wing melanic-infusate in distal half only; tergum 3 wider than tergum 2 *S. rufiabdominalis* He and Chen
- 9. Vertex of head and apex of hind tibia black (southern Africa) *S. fulvus* Brues.
- 9'. Head and hind tibia entirely reddish brown (Madagascar) *S. testaceus* Granger.

Sigalphus romeroi Sharkey n. sp.
(Figs 2a, d, 3a, b)

MALE.

Length.—8.4 mm.

Color.—Entirely black except fore tarsus brown, wings evenly infusate.

Head.—Antenna with 42–44 flagellomeres.

Mesosoma.—Pronotum smooth except for weak crenulae along posterior border; subpronope present; notaulus deeply impressed and with weak punctures; scutellar furrow (sulcus) smooth except for median longitudinal carina; posterior scutellar depression composed of two large pits; median depression of metanotum semicircular (rounded posteriorly); propodeum entirely areolate, with pair of strong longitudinal carinae defining medial area; sternaulus complete to epicnemial carina; fore wing (Fig. 3a) with veins M and m-cu not distinctly converging anteriorly; crossvein a of fore wing not present; sec-

ondary crossveins r and m-cu of hind wing present though weak and not tubular (Fig. 3b).

Metasoma (Figs 2a, d).—All terga rugose; first tergum with two precurrent longitudinal carinae; second tergum with median longitudinal carina, and without deep anterolateral depressions (as in *S. bicolor*); tergum 3 lacking long dense setae; ventral margins of carapace crenulate; apex of ventral metasomal foramen with 6 ridges forming weak, sharp, denticles (Fig. 2a); ventral foramen of carapace not extending to apex of metasoma, i.e., tergum 3 curved around apex of metasoma forming posterior surface.

Material Examined.—Holotype male: COSTA RICA, Guanacaste Province, Guanacaste Conservation Area, Sector Santa Rosa; 300 m. Janzen rearing data base voucher number 90-SRNP-828. Larval host *Epithisanotia sanctijohannasi* (Noctuidae) collected 24 June 1990, wasp

eclosed 26 May 1991. Instituto Nacional de Biodiversidad (INBio), Santo Domingo de Heredia, Costa Rica.

Paratype male: COSTA RICA, Guanacaste Province, Guanacaste Conservation Area, Sector Santa Rosa, 300m. Janzen rearing data base voucher number 92-SRNP-2777. Larval host *Erochia mummia* (species complex) (Noctuidae) collected 7 July 1992, wasp enclosed 10 May 1993. Canadian National Collection, Ottawa, Canada.

Remarks.—The female of this species is unknown. *S. romeroi* is easily distinguished from the only other New World species, *S. bicolor* by the characters given in the key.

Etymology.—The species is named in honor of Sra. Luz Maria Romero in recognition of her outstanding drive and inspiration in guiding and developing the Biological Education Program of the Guanacaste Conservation Area in northwestern Costa Rica.

Biogeographical Notes.—This is the first record of members of the genus *Sigalphus* in the Neotropics and only the second species to be discovered in the New World. The genus is unknown in South America.

As suggested in the section on phylogeny, the non-Ethiopian members of *Sigalphus* may be monophyletic based on the presence of denticles at the ventroposterior margin of tergum 3. If this is so, the distribution of the New World species is interesting from a biogeographic perspective.

It is generally agreed that the closest phylogenetic relationships of most temperate North American taxa are found in the northern hemisphere of the Old World (Lavin and Luckow 1993). In contrast the usual hypothesis put forward to explain North American tropical fauna is dispersal from South America.

If the non-Ethiopian members of *Sigalphus* are monophyletic, it suggests a northern hemisphere origin of *S. romeroi*, the only Neotropical member of the genus. This distribution is consistent with what

has been referred to as the boreotropics hypothesis, which suggests a historically more widespread tropical northern hemisphere biota. (Wolfe 1975; Tiffney 1985a, b; Lavin and Luckow 1993).

Biology.—The larval hosts, *Epithisanotia sanctijohannasi* and *Erochia mummia* (both: Noctuidae, Agaristinae), are common to exceedingly rare (depending on the year) and univoltine in the primary to early successional dry forests in eastern Sector Santa Rosa of the Guanacaste Conservation Area in northwestern Costa Rica (200–300m elevation; about 35 km north of the town of Liberia, to the west of the Interamerican Highway) (see Janzen 1987, 1988a, 1988b, 1993 for a general site description of this forest and its caterpillars). *E. sanctijohannasi* and *E. mummia* are most easily located when they are feeding on the large woody vine *Tetracera volubilis* (Dilleniaceae, Dilleniales) (hundreds of records), and *E. sanctijohannasi* has also been found feeding on *Curatela americana* (4 records). These larvae eat mature leaves and are non-gregarious feeders in the penultimate and ultimate instars (earlier instars unknown) on both host plants. Both species are univoltine (last instar caterpillars occurring in late June and early July, the second and third months of the rainy season) and the pupae remain dormant through the remainder of the six month rainy season and all of the dry season, with the moths eclosing in May at the beginning of the rains (see Janzen 1987, 1988a, 1993 for other examples of the same phenomenon).

Of 36 *E. sanctijohannasi* 31 *E. mummia* last instar larvae collected and reared from *T. volubilis* in 1992 and 1993, 84 and 93 percent respectively produced last instar larvae of *Sigalphus romeroi*. This extremely high percent of parasitization is not representative of caterpillar-parasitoid interactions in this forest, where 1–30% parasitization by a given species of parasitoid is usually recorded (D. H. Janzen, unpublished rearing records). The very large

number of *Sigalphus romeroi* larvae did not generate a large paratype series because, as explained below, the larvae proved to be very incompetent at spinning cocoons and surviving subsequently under artificial rearing conditions.

The parasitized last instar caterpillars of *E. sanctijohannasi* and *E. mummia* appear to be perfectly normal in feeding, fleeing and walking behaviour. The prepupal caterpillar searches in the litter for a piece of rotting wood, tunnels into the wood, and makes its pupal chamber there. Within 1–3 days of the caterpillar entering the wood the wasp larva eats nearly all of the contents of the prepupal caterpillar and exits the cadaver. The wasp larva is so large that there does not appear to be sufficient food for more than one per caterpillar of either host. The wasp larva then spins an ovoid white cocoon in the caterpillar's pupal chamber (late June to early July), where it remains dormant as a prepupal larva until the following May, when it pupates and exits through a round hole cut in the cocoon, and then burrows out through the wood chip-filled entrance tunnel made initially by the caterpillar.

The biology described in the previous paragraphs is based on observation of all of this behaviour with captive caterpillars individually confined in large plastic bags and bottles in an open air laboratory a few meters from the forest where the caterpillars and wasps are found naturally. Dormancy of moth pupae and of wasp larvae in their cocoons occurred in the individuals confined under three conditions of captivity, i.e., under moist conditions throughout the wet season with a change to dry conditions during the dry season, entirely under dry conditions throughout the wet and dry seasons, and for those captured in the dry season they remained in a dry environment in captivity. Moths in the pupal stage and wasp larvae both use some environmental cue that is perceivable through the walls of a plastic bag to initiate further development in late

April or early May, and this cue is most likely the abrupt drop in temperature that accompanies the first rains (see Janzen 1993). By eclosing at the same time as the moths, the adult wasps are presumably present at exactly the same time as are the first instar larvae of the next generation of caterpillars which, extrapolating from the known biology of *S. bicolor*, is the stage most likely to be attacked.

The larva of *Sigalphus romeroi* is exceptional, among the species of parasitoid wasps that the junior author has reared in this forest, in its inability to spin a cocoon except in the pupal chamber of its host. It was usually not able to spin a cocoon between leaves in the litter, among crumpled layers of dry or moist toilet tissue, or in tubular chambers of toilet tissue. Of ten larvae that did succeed in spinning cocoons among toilet tissue layers, all died of unknown causes over the following seven months.

Malaise traps run for the equivalent of tens of years in this dry forest between 1984 and 1988 (e.g., Gauld 1988, Gaston and Gauld 1993) have captured no specimens of *S. romeroi* (I. D. Gauld and P. A. Mitchell, personal communication). This result is particularly striking given that the Malaise traps were located within several meters of the host plants and in all ages of forest succession.

In contrast to *S. romeroi* being large, solitary, and univoltine, *Sigalphus bicolor*, the only North American member of the genus, is small, gregarious and multivoltine. *S. bicolor* oviposits in the first instar larvae of a noctuid caterpillar, *Acronicta clarescens* (= *Apatela clarescens*), and the larvae come out of the prepupal caterpillar and spin their cocoons within the host cocoon (Cushman 1913, who described the wasp's natural history under the name *Sphaeropyx bicolor*). The only western Palearctic species of the genus, *S. irrorator* has also been reared from *Acronicta* in Europe, but because of its large size (about the same as *S. romeroi*) it is inferred to be solitary (*S.*

Ward, personal communication). You, Zhou and Tong (1991) report *S. irrorator* (as *S. anomis*) as a parasitoid of *Anomis flava* (Noctuidae). The biology of all other species of *Sigalphus* is unknown.

Sigalphus masoni Sharkey n. sp.
(Figs. 2b, c, 3c)

HOLOTYPE FEMALE.

Length.—10.9 mm.

Color.—Mostly black with yellow on bases and ventral sides of all tibiae and on metasomal sterna, and orange on metasomal terga 1, 2, and anterior $\frac{2}{3}$ of tergum 3; fore wing entirely infuscate though somewhat paler basally; hind wing clear in basal $\frac{1}{3}$, infuscate in distal $\frac{2}{3}$.

Head.—Antenna broken.

Mesosoma.—Pronotum weakly rugose; subpronope present; notaulus deeply impressed and crenulate; scutellar furrow (sulcus) smooth except for three longitudinal carinae; posterior scutellar depression composed of many small pits; median depression of metanotum sharply triangular (acute posteriorly); propodeum weakly rugose laterally with pair of longitudinal carinae defining medial area; sternaulus complete to epicnemial carina; fore wing with veins M and m-cu distinctly converging anteriorly; crossvein a of fore wing present and distinct; hind wing with secondary crossvein r present and secondary crossvein m-cu absent.

Metasoma (Figs 2b, c).—All terga rugose; first tergum with two precurrent longitudinal carinae; second tergum with median longitudinal carina and an equally strong pair of lateral longitudinal carinae that converge towards the mid-line posteriorly; second tergum with moderately deep anterolateral depressions (as in *S. bicolor*); tergum 3 with long dense setae; ventral margins of carapace crenulate; apex of ventral metasomal foramen with two rounded denticles (Fig. 2c); ventral foramen of carapace (Fig. 2c) not extending to apex of metasoma.

Material Examined.—Holotype ♀: NE-

PAL: Katmandu, Godavari, 5,000 ft. (1524 m.), 6.VIII.1967, Canadian Nepal Expedition, [Canadian National Collection, Ottawa, Canada]

Biology.—Unknown

Remarks.—Members of *S. masoni* are similar to those of *S. irrorator* and *S. mongolicus* in some respects, particularly in their general size and the long setae on metasomal tergum 3. In *S. masoni*, these setae are longer and denser than in the New World species of *Sigalphus*, though they are not as exaggerated as those of *S. irrorator*, nor are they gold colored. Members of the two species differ in color, those of *S. masoni* having the metasoma predominantly orange versus entirely black in *S. irrorator*. The species also differ in the shape of the denticles at the apex of the ventral foramen, i.e., those of *S. masoni* are wide and blunt whereas those of *S. irrorator* and *S. mongolicus* are relatively narrow and acute. The most distinctive feature distinguishing *S. masoni* from other species of *Sigalphus* is the sculpture of the second metasomal tergum. All other Palearctic and Oriental species of *Sigalphus* have a median longitudinal groove bordered laterally by longitudinal carinae. These are not present in *S. masoni* (Fig. 2d).

Etymology.—The species is named after Dr. W. R. M. Mason for his many contributions to Hymenopterology, and also, though it is not stated on the label, because he is thought to be the collector of the unique specimen.

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Jason Hardis drew the fore wing *S. masoni*. All other drawings were done by Barry Flahey. We thank David Althoff, Paul Marsh, Lubomir Masner, Eric Rickney, Ales Smetana and two anonymous reviewers for valuable comments on early drafts.

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